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Bottom-up effects of lake sediment on pelagic compartments: a mesocosm study

Loïc Harrault[1,2,3,#], Béatrice Allard[1], Jacques Mériguet[3], David Carmignac[3], Sylvain Huon[1], Benoit Gauzens[3,4] and Gérard Lacroix[5,6]

[1] Université Pierre et Marie Curie, UMR CNRS 7618 - Bioemco, 4 place Jussieu, 75252 Paris Cedex05, France

[2] Université Rennes 1, UMR CNRS 6118 - Géosciences Rennes, Campus de Beaulieu, 35042 Rennes Cedex, France

[3] Ecole Normale Supérieure, UMR CNRS 7618 - Bioemco, 46 rue d'Ulm, 75005 Paris, France

[4] Université Rennes 1, UMR CNRS 6553 ECOBIO, Campus de Beaulieu, 35042 Rennes Cedex, France

[5] CNRS, UMR iEES - Paris, Institute of ecology and environmental sciences - Paris, Université Pierre et Marie Curie, 7 quai St.-Bernard, 75005 Paris, France

[6] Ecole Normale Supérieure, UMS CNRS 3194 - CEREEP – Ecotron IleDeFrance, 78 rue du Château, 77140 St-Pierre-lès-Nemours, France

corresponding author : loic.harrault@gmail.com

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Abbreviated title: Influence of lake sediment on pelagic compartments

Summary

1. Sediment plays a key role in organic matter (OM) and internal nutrient cycling in lakes. The role of sediment as a source of OM, and its potential bottom-up effects on the pelagic food web have been rarely studied. Particularly, the influence of the biochemical composition of sediment OM on pelagic compartments remains largely unknown.

2. In a five-months experiment, we studied the influence of two different sediments added at the bottom of large replicated mesocosms on the biomass, the elemental and the lipid compositions of seston and zooplankton. The influence of sediment treatments on sedimentation rates, elemental and biochemical compositions and potential biodegradability of recently sedimented OM (ca. 1 week) was also examined. The two added sediments (S_1 and S_2) presented very contrasted elemental and biochemical compositions and potential biodegradabilities. According to their contents in organic carbon, nitrogen, proteins, sugars and polyunsaturated fatty acids, S_2 appeared to be much more biodegradable than S_1. Therefore, the S_2 sediment was expected to release more nutrients and OM to the water column than S_1, leading to changes in communities, stoichiometry and lipid compositions of pelagic compartments.

3. Probably due to its very poor content in labile compounds, the presence of S_1 at the bottom of the mesocosms did not induce changes in the biomass of seston and zooplankton. Only few changes in the stoichiometry of these compartments were observed. On the contrary, S_2 sediment released more phosphorus and dissolved OM in the water column than S_1. As a result, S_2 treatment induced an increase in seston biomass and therefore, in zooplankton biomass *via* herbivory.

4. None of the sediment treatments affected the lipid composition of seston and zooplankton. Moreover, neither S_1 nor S_2 induced changes in the sedimentation rates, elemental and lipid compositions, and potential biodegradability of recent sediments. Our mesocosm experiment suggests that differences in the quality of lake sediment lead to moderate changes in the pelagic communities in the absence of planktivorous or omnivorous fish.

5. Our results might explain the efficiency of biomanipulations for improving water quality of eutrophic lakes despite potential nutrient release from sediment. Finally, our results provide additional support for the ecological significance of mesocosms for studying processes occurring at larger scales.

Introduction

Since a few decades, the role of sediment in the biological and biogeochemical processes in lacustrine ecosystems has received an increased attention. Lipid composition of sedimented organic matter (SOM) has been widely used to assess, via specific biomarkers, i) autochthonous *vs* allochtonous origin of sediment (Canuel & Martens, 1993; Bechtel & Schubert, 2009; Castaneda & Schouten, 2011), ii) transfers of energy and nutrients between primary producers, herbivores and other consumers within aquatic food webs (Müller-Navarra *et al.*, 2000; Masclaux *et al.*, 2009) or iii) inter-specific differences (Volkman *et al.*, 1988; Cranwell *et al.*, 1990). The sediment geochemistry has also been used to study the carbon balance in lacustrine ecosystems and its contribution to the global carbon cycle (Alin & Johnson, 2007; Cole *et al.*, 2007). The net heterotrophy of lakes (CO_2 source for atmosphere) is the most commonly observed carbon fate in concerned studies (del Giorgio *et al.*, 1997; Cole *et al.*, 2000). It has been shown that this balance can be influenced by food-web structure, nutrient concentration (Schindler *et al.*, 1997), or climate (Kosten *et al.*; 2010), which, in turn, modifies sedimentation (Flanagan *et al.*, 2006). Furthermore, several recent studies in both marine mesocosms (Canuel *et al.*, 2007; Spivak *et al.*, 2007) and freshwater mesocosms (Allard *et al.*, 2011; Danger *et al.*, 2012), have shown that the biochemical composition (e.g. organic carbon, protein, sugar and lipid contents) of recently deposited sediments depends on food-web structure.

Once sedimented, OM is subject to transformation and biodegradation by benthic macroinvertebrates (Mermillod-Blondin *et al.*, 2003; Nogaro *et al.*, 2008) and microorganisms (Gächter *et al.*, 1988; Hargreaves, 1998). Biodegradation depends on several parameters, such as dissolved oxygen concentration at the sediment-water interface, binding on mineral matrix (Wakeham & Canuel, 2006), physical resuspension (Sanford, 1992), or OM composition (Hulthe *et al.*, 1998). This latter has been largely used to provide information on

the degradation state and the biodegradability of the sediment, due to the large range of lability covered by the different components of OM (Meckler *et al.*, 2004; Schubert *et al.*, 2005). During its degradation, the sediment can release into the water column nutrients and dissolved organic matter (DOM; Reynolds, 1996; Klump *et al.*, 2009), which will support both primary and bacterial productions (del Giorgio & Cole, 1998). As phytoplankton and bacteria are the basal resources for aquatic food webs, release of nutrients and OM from sediment might strongly impact food-web communities via a bottom-up forcing. Whereas the bottom-up effects of inorganic nutrients or light on aquatic ecosystems are well known (see for example, Urabe *et al.*, 2002; Cebrian & Lartigue, 2004; Hessen *et al.*, 2004; Dickman *et al.*, 2006; Spivak *et al.*, 2007), those of SOM have been more rarely studied. In natural lakes, it has been shown that the temporal dynamics of bacterioplankton communities are strongly dependent on the DOM origin and amount (Berdjeb *et al.*, 2011), suggesting a bottom-up forcing from DOM. As DOM can originate from sediment biodegradation, one may wonder if sediment could be responsible for a bottom-up control for the whole food web, through the availability of resources for basal organisms (e.g. phytoplankton and bacterioplankton). Moreover, as the sediment biodegradability seems to be linked to its OM composition (Allard *et al.*, 2011; Danger *et al.*, 2012; Harrault *et al.*, 2012), an interesting issue is whether different sediment compositions could lead to different bottom-up forcing on aquatic food webs.

In this paper, we report results of a lake mesocosm study examining how the presence and the OM composition of sediment can exert a bottom-up effect on the composition of seston, zooplankton and recently deposited (ca. 1 week) sediment. Three treatments were compared: enclosures without added sediment (S_0), enclosures with carbon-poor sediment (S_1), and enclosures with carbon-rich sediment (S_2). Sediment S_1 was taken in the bottom of Lake Créteil (Lacroix & Lescher-Moutoué, 1995), while S_2 came from a previous mesocosm

experiment (Danger *et al.*, 2008, 2012) and was composed of OM from pelagic origin, settled down during a few years in large pelagic enclosures. The compounds that are preferentially degraded by bacteria, such as polyunsaturated fatty acids (PUFAs, Cranwell, 1981), and sugars and proteins (Weiss & Simon, 1999), were much more abundant in S_2 than in S_1 (Table 1). This strongly suggested that S_2 was much more biodegradable than S_1. Indeed, S_1 had been formed over several decades in a shallow gravel-pit lake with a clear tendency to oligotrophication since the end of its exploitation (Garnier, 1992). In contrast, the composition of S_2 was typical of sediments found in hypereutrophic conditions (Søndergaard, 1988), in aquaculture areas (Yokoyama *et al.*, 2009), and in extensive fish ponds (Banas *et al.*, 2008).

During 5 months, the biomass and the elemental composition of pelagic compartments were determined. At the end of the experiment, the lipid composition of the biotic compartments was determined. According to the results of Spivak *et al.* (2007), Allard *et al.* (2011), Danger *et al.* (2012) and Harrault *et al.* (2012), we hypothesised that:

(i) a positive bottom-up forcing from sediment would increase the biomass of seston (direct effect through the ingestion of released OM and/or nutrients) and the biomass of zooplankton (indirect effect through the ingestion of increased seston biomass);

(ii) the strength of this bottom-up effect would depend on the OM composition of the bottom sediment: $S_0 < S_1 < S_2$ (i.e. the more biodegradable a sediment, the greater the bottom-up forcing);

(iii) this effect could change the stoichiometry and/or the lipid biomarker composition of pelagic compartments by modifying nutrient balances.

Methods

Study site, experimental design and choice of bottom sediments

This study took place in Lake Créteil (48°46'37''N, 2°26'47''E), a small (42 ha), shallow (mean depth 4 m) sandpit lake 15 km southeast of Paris, France (for more information on this lake, see Danger *et al.*, 2008). Twenty-four translucent polyethylene enclosures, sealed at the bottom, were suspended above the lake surface on a floating pontoon. The volume of each enclosure was ca. 13.5 m^3 (2 × 1.5 × 4.5 m depth). At the end of November 2009, enclosures were randomly filled in successive steps with pumped lake water. To study the bottom-up effects of initial sediment on pelagic compartments and on recently deposited sediment, two contrasted sediments were set down at the bottom of the enclosures. Enclosures without added sediment were used as a control (S_0). Each treatment was replicated eight times. The first sediment (S_1) was collected randomly in Lake Créteil with an Uwitec bottom sampler and consisted of a dark grey sandy material. The second sediment (S_2) was collected in enclosures used in a previous study (Danger *et al.*, 2008, 2012). S_1 and S_2 were chosen to simulate contrasted bottom-up treatments in enclosures. Both autochthonous and allochthonous sources contributed to S_1. This sediment had been accumulated and exposed to microbial and benthic reworking over several decades. In contrast, S_2 was sampled in enclosures sealed at their bottom and largely preserved from allochthonous inputs, and therefore mainly of autochthonous origin. Moreover, this sediment is relatively young since it was collected in experimental mesocosms set up in 2005 (Danger *et al.*, 2008) and has been exposed to degradation over a shorter period than the sediment of the lake. The difference in the initial sediment quality was estimated using the sugar, protein and PUFA contents (Table

1). The difference in the degradation state of the initial sediments was estimated using their bacterial fatty acid (BACTFA), α- and β-hydroxy fatty acid (OH-FA) and stanol contents (Supplementary Table 1).

Once collected, sediments (ca. 600 L each) were pooled into 200-L tanks for homogenisation. Trays (2 × 1.5 m), filled with ca. 70 L of homogenized sediment (ca. 2.4 cm depth layer), were lowered very slowly at the bottom of each enclosure to minimize sediment resuspension and subsequent dissolution of nutrients and OM. Empty trays were put in the control enclosures. To allow sedimentation of suspended material in S_1 and S_2 enclosures, we started samplings on February 2010.

Orthophosphates, ammonium and nitrates analyses

Orthophosphate, ammonium and nitrate concentrations were determined for water sampled in May and June 2010 using the phosphorus-ammonium molybdate and the indephenol blue spectrometric methods, respectively (AFNOR, 1990, 2004).

Dissolved organic carbon analysis

Water samples collected in May 2010 were filtered through a Whatman GF/F filter. Dissolved organic carbon (DOC) concentration was determined using a total organic carbon analyser (TOC-5000A, Shimadzu, Kyoto, Japan).

Seston and zooplankton sampling

Seston biomass and elemental composition were determined monthly. Water was sampled monthly from February to June 2010 at different depths and locations with a 2-L sampling bottle (Uwitec) in each enclosure. Water samples were filtered through a 50-µm nylon filter to remove zooplankton, and then filtered through a pre-weighted Whatman GF/F glass-fiber filter (nominal cut-off: 0.7 µm) in order to gather seston (particulate matter between 0.7 and 50 µm). Filters were dried overnight at 60°C and weighted to determine seston biomass. Dry filters were stored in the dark at room temperature until elemental and lipid analyses. Zooplankton biomass was determined monthly by sampling 60 L of water at different depths and locations in each enclosure with a 12-L Schindler plankton trap equipped with a 50-µm filter. Zooplankton was gathered in GF/F-filtered water for several hours to allow evacuation of gut content. Zooplankton was concentrated on a 50-µm filter, washed with deionized water to remove particles and dissolved matter bound to their shell, placed on a pre-weighted Whatman GF/A glass-fiber filter (nominal cut-off: 1.6 µm), and dried overnight at 60°C. Dry zooplankton was ground and stored in the dark at room temperature until elemental and lipid analyses.

Zooplankton counting

Zooplankton composition was determined in February and May 2010 by filtering 60 L of water at different depths and locations in three enclosures of each treatment with a 12-L Schindler plankton trap equipped with a 50-µm filter. Zooplankton was preserved in 4%

formaldehyde. Zooplankton taxa were identified and counted under a Leica stereo-microscope on subsamples at different dilutions in Dollfuss chambers. Copepods were separated into cyclopidae, calanoida and nauplii. Cladocera were separated into *Daphnia*, *Ceriodaphnia*, and Chydoridae. Rotifers were counted globally.

Sampling of recent sediment

Recently deposited sediments were sampled in May and June 2010. Sedimentation rates were determined using six sediment traps deployed in each enclosure. Traps consisted of 5-cm diameter and 30-cm long PVC tubes, suspended at 4 m depth. Suspended 0.5 m above the bottom of the enclosures, sediment traps were preserved for bottom sediment resuspension. Traps were deployed for 7- to 9-day intervals. Material collected from the six traps was pooled in a collection flask and allowed to sediment overnight at 4°C. The supernatant and zooplankton therein was removed. Sediment was freeze-dried, weighted, ground and stored in the dark at room temperature until analyses. Sedimentation rates were calculated as the mass of dry matter divided by the duration of the trap deployment and the total surface of the six traps, and expressed in g m^{-2} day^{-1}.

Elemental composition of seston, zooplankton, initial and recent sediment

Carbon and nitrogen contents of dried samples were determined using a CHN elementary analyzer (FlashEA 1112 series, Thermo Fisher Scientific) with acetanilide as standard. Initial

and recent sediment organic carbon contents (OC) were determined after removal of inorganic carbon (IC) from sediment by successive additions of 1 M HCl (Hedges & Stern, 1984).

Sugar and protein colorimetric assays of sediments

Freeze-dried sediments were extracted with H_2O at 100°C for 2 h. The mixture was filtered through a Whatman GF/F filter, and the filtrate was freeze-dried. The freeze-dried aqueous extract was dissolved in a known volume of H_2O and assayed for sugars and proteins. Sugar contents were determined using the phenol–sulfuric acid colorimetric method with glucose as standard (Dubois *et al.*, 1956). The protein contents were determined using the colorimetric method of Lowry with bovine serum albumin as standard (Lowry *et al.*, 1951). Sugar and protein contents were expressed as percentages of the sediment dry weight (DW).

Lipid analysis

All chemicals used were of analytical grade.

Apart from initial sediments S_1 and S_2, analyses of lipids were carried out on three replicates of each treatment for seston, zooplankton and recent sediment sampled in May 2010.

The filter with collected seston was extracted with a dichloromethane (DCM)/methanol (MeOH) (2/1, v/v) mixture at room temperature for 18 h. The mixture was filtered through a Whatman GF/F glass-fiber filter and solvent was removed under reduced

pressure. Extracts were saponified at 80°C for 2 h with 1 M KOH in MeOH. The pH of saponified extract was brought to 2 by addition of 6 M HCl and lipids extracted with DCM. The organic phase was washed with deionized water until neutral pH, dried over Na_2SO_4 and DCM removed under reduced pressure. Saponified lipids were treated with ca. 4 M HCl in MeOH at 80°C for 1 h to convert carboxyl groups into their methyl ester derivatives. Esterified extract was then treated with a mixture of anhydrous pyridine/N,O-Bis(trimethylsilyl)trifluoroacetamide (BSTFA) (10/1, v/v) for 10 min at 60°C to convert hydroxyl groups into trimethylsilyl (TMS) ether groups. Lipid components (as methyl esters and TMS ethers) were analysed by gas chromatography-mass spectrometry (GC–MS) with an Agilent 6890 gas chromatograph coupled to an Agilent 5973N mass spectrometer with electron ionization at 70 eV. Separation was achieved using a fused silica column coated with RTX5SilMS (30 m, i.d. 0.25 mm, film thickness 0.5 µm) with helium as carrier gas. The GC oven was programmed from 100 to 320°C at 4°C min^{-1}. Unsaturated fatty acids were analysed using gas chromatography-flame ionization detector (GC-FID) and identified by comparison with standards (Larodan, Malmö, Sweden) using fused silica column coated with DB23 (60 m, i.d. 0.25 mm, film thickness 0.25 µm) with helium as carrier gas. The GC oven was programmed from 100 to 170°C at 6.5°C min^{-1}, then to 215°C at 2.75°C min^{-1} and to 230°C at 40°C min^{-1}. Individual component contributions were determined by comparison of the peak areas from GC–MS traces. This method allowed a comparison of the relative abundance of each compound between the different samples analysed, but did not allow the quantification of individual compounds within the total lipids. Dried zooplankton samples were extracted and lipids analyzed as described for seston. The amounts of extracted lipids were too low to allow an accurate weight determination.

Freeze-dried sugar- and protein-free sediment samples were extracted with a chloroform/MeOH (2/1, v/v) mixture for 2 h at 80°C. Lipid extracts were analysed as described for seston.

Statistical analyses

Statistical analyses were performed using R software (www.r-project.org). A linear mixed-effects model (LME) with sediment treatment, time and cross-effect as explanatory variables and replicates as a random effect was used to test the individual and the combined effects of sediment treatment (S_0, S_1 and S_2) and time on the biomass of seston and zooplankton (from February to June), zooplankton composition (February and May), sedimentation rates (May and June), elemental compositions of seston, zooplankton (from February to June) and recent sediment (May and June), and orthophosphate, ammonium and nitrate concentrations of water (May and June). For response variables analysed only in May (DOC and lipid biomarkers), effects of sediment treatment were tested with a LME with sediment treatment as explanatory variable and replicates as a random effect. Post-hoc Tukey's tests (Tukey) were performed to compare one treatment to another. Data were log-transformed when necessary to homogenize distributions and variances.

Technical constraints

The design of this experiment had been initially planned to last for almost 2 years and not for 5 months as presented here. With the design initially conceived, regular sampling on various

biotic and abiotic parameters were planned from May 2010 to December 2011. Unfortunately, extreme climatic events have damaged the enclosures, forcing us to stop the experiment on July 2010 with an incomplete and heterogeneous set of data. As a consequence, phosphorus analyses in the various compartments of the mesocosms were not possible, and other analyses (nutrients, DOC, particles, zooplankton taxonomy) were conducted only on one or two sampling dates.

Results

Water: nutrient and DOC concentrations

In May and June, sediment treatment had a significant effect on orthophosphate concentration of water (Table 2). Orthophosphate concentration from S_2 enclosures was significantly higher than those from S_0 and S_1 enclosures, which did not differ significantly each other.

Sediment treatment had no significant effect on the concentrations of ammonium and nitrates and on the inorganic nitrogen (sum of ammonium and nitrate concentrations)/orthophosphates ratio (IN/P, Table 2). Despite this absence of significant effect, a IN/P ratio from S_2 enclosures (5) much lower than that from both S_0 and S_1 (16 and 18, respectively) was observed.

In May, sediment treatment had a significant effect on DOC concentration (Table 2). DOC concentration in S_2 enclosures was significantly higher than that in S_1 enclosures. In

contrast DOC concentration in S_0 and S_1 enclosures did not differ significantly and DOC concentration in S_2 enclosures did not differ significantly from that in S_0 enclosures.

Seston: biomass and elemental composition

Biomass and elemental compositions of seston (particulate matter between 0.7 and 50 µm) from the different treatments were reported in Table 2.

Sediment treatment had a significant effect on seston biomass (Fig. 1a) since, on average, seston biomass in S_0 and S_1 enclosures did not differ significantly but were lower than those from S_2 enclosures. Seston biomass was higher during winter than during spring.

The C content of seston did not differ significantly among treatments and was slightly higher on April than for the other dates (Fig. 2a). The N content of seston was affected by sediment treatment: it did not differ between S_0 and S_1 enclosures but was lower in S_0 enclosures compared to S_2 enclosures, without any time effect (Fig. 2b). The C/N ratio of seston from S_0 treatment was higher than that of seston from S_1 and S_2 treatments but this difference was only observed in February and March (Fig. 2c). The C/N ratio of seston was lower in February than during the following months.

Zooplankton: biomass, specific and elemental compositions

Biomass and elemental compositions of zooplankton from the different treatments were reported in Table 2.

Sediment treatments had a very significant effect on zooplankton biomass (Fig. 1b). On average, zooplankton biomass did not differ significantly between S_0 and S_1 enclosures but was higher in S_2 enclosures than in S_0 and S_1 ones, especially in March and April (Fig. 1b). Zooplankton biomass increased from February to April and then decreased up to June.

Species composition of zooplankton communities was weakly affected by sediment treatments since only the concentration of Chydoridae was significantly higher in the S_2 enclosures than in S_0 and S_1 ones (Table 4). On average, the number of individuals was lower in February than in May, especially for nauplii of copepods (7.3 ± 3.4 and 180.9 ± 77.7 individuals L^{-1}, for February and May, respectively. C and N contents and C/N ratio of zooplankton from S_0, S_1 and S_2 treatments did not differ significantly (Table 2). The C content of zooplankton slightly increased from February to March and then slightly decreased until June (Fig. 3a). The N content of zooplankton sampled in February was lower than that sampled on the other dates (Fig. 3b). The opposite trend was observed for the C/N ratio of zooplankton (Fig. 3c).

Recent sediment: sedimentation rates, elemental compositions and sugar and protein contents

Recent sediments were sampled in May and in June. Sedimentation rates and elemental composition of recent sediments were reported in Table 2.

Sediment treatments and time did not significantly affect the sedimentation rates (Fig. 1c), although sedimentation rates tended to be higher in S_1 and S_2 than in S_0 enclosures.

Sediment treatments affected the C, OC and N contents of recent sediments since those from S_1 enclosures were lower than those from S_0 and S_2 ones (Fig. 4a and 4b). The

C/N ratio of recent sediment from S_1 treatment was higher than that from S_0 and S_2 treatments (Fig. 4c). In contrast, the OC/N ratio was not significantly affected by the sediment treatment.

The amount of sugar and protein contents of recent sediments did not differ significantly between the different treatments (Table 2).

Lipid compositions of seston, zooplankton and recent sediments

Mean lipid distributions of the three pelagic compartments were reported in Table 3.

Except for chlorophyll-derived compounds in recent sediments (LME: p = 0. 026, $F_{2,6}$ = 7.13), sediment treatments had no significant effect on the relative amounts of the different lipid classes of seston, zooplankton and recent sediments (data not shown). Chlorophyll-derived compounds were more abundant in recent sediments from S_2 (4.7 ± 1.7 % of total lipids) enclosures than in recent sediments from S_0 (1.8 ± 0.7 % of total lipids, Tukey: p = 0.033) and S_1 (2.0 ± 0.5 % of total lipids, Tukey: p = 0.048) enclosures. FAs largely dominated their lipid distributions, followed by alkanols. Sterols, hydroxy acids and chlorophyll-derived compounds were present in lower relative abundances.

Sediment treatments had no effect on the FA distributions (Supplementary Tables 1 and 2). For all treatments saturated fatty acids (SAFAs) dominated the distribution, followed by monounsaturated fatty acids (MUFAs), PUFAs (long-chain PUFAs, carbon number ≥ 20, accounting for ca. 1, 27 and 8% of total PUFAs for seston, zooplankton and recent sediments, respectively) and BACTFAs.

Sterol distributions did not depend on sediment treatment (Table 3). For all treatments, 24-ethyl-cholest-5-enol ($C_{29}\Delta^5$) and cholesterol ($C_{27}\Delta^5$) largely dominated the sterol distribution of recent sediments, with stanols accounting for less than 2% of total sterols.

Discussion

All the criteria used for the selection of the bottom sediments suggest that the potential biodegradability of S_2 could have been one order of magnitude higher than that of S_1. The pool of OM, which represented the total stock of resources potentially used by bacteria, proteins and sugars, essential for bacterial growth, and PUFAs, preferentially degraded by bacteria, were clearly more abundant in S_2 than in S_1.

Effects of bottom-up forcing on pelagic compartments

According to the characteristics of S_1 and S_2, a release of nutrients and OM in the water column in the order $S_0 < S_1 < S_2$ was expected. We hypothesized that this would lead to an enhanced bottom-up forcing on the basal organisms of the food web, resulting in an increase of seston biomass. By consuming seston, zooplankton was also expected to increase its biomass with addition of sediment of increasing biodegradability. The phosphate and DOC concentrations in the water column as well as the biomass values of seston and zooplankton, all higher in S_2 treatment than in S_1 and S_0 treatments, partially corroborated this hypothesis.

The sediment of S_2 enclosures, which was typical of eutrophic to hypertrophic lakes and fishponds (Søndergaard, 1988; Banas *et al.*, 2008), clearly fostered pelagic compartments.

This result confirms that eutrophic ecosystems are subject to internal nutrient loading, and that released nutrients may be taken up by aquatic food webs (Søndergaard *et al.*, 2003, 2007). Interestingly, the experiment was run from December to June, when dissolved oxygen remained oversaturated in all enclosures, even near sediments (data not shown). This strengthens the statement of Nürnberg (2009) that "phosphorus release is not restricted to and does not require anoxia in the overlaying water". As for dissolved oxygen, we did not find any significant treatment effect on the pH values in the water column, which were high and ranged between 8.1 and 8.5 (data not shown). Such values are considered to favour phosphorus release from sediment (Koski-Vahala & Hartikainen, 2001). Other processes may have favoured nutrient transfer into the overlaying water of S_2 enclosures. Activity of benthic micro- and macroinvertebrates is probably one of these mechanisms, as suggested by the higher abundance of Chydoridae in microinvertebrate samples and by the frequent observation of Chironomids in the S_2 enclosures (direct observations). Moreover, a higher microbial mineralisation of the highly biodegradable S_2 SOM was expected (Gächter & Meyer, 1993; Pettersson, 1998). The observed changes in dissolved nutrients in water and associated biomass of seston suggest a limitation of planktonic primary producers by phosphorus in S_0 and S_1 enclosures, and a reduction of such P-limitation, accompanied by a higher primary productivity, in S_2 enclosures. It would be interesting to conduct long-term experiments in order to verify how internal nutrient loading associated to sediment-water exchanges may change nutrient limitation of phytoplankton in a seasonal context.

By contrast, no difference was observed in the nutrient and DOC concentrations, and in the biomass of seston and zooplankton between S_1 and S_0 treatments. This absence of significant difference between S_1 and S_0 suggests that the potential bottom-up effect associated to OM degradation and nutrient release from the sediment of Lake Créteil was limited. As highlighted previously (Lacroix *et al*. 1989), the lack of OM accumulation in the

sediment of this shallow sand-pit lake, despite high lake productivity, suggests an efficient OM transfer within the pelagic food web and an efficient nutrient recycling within the water column. The low initial abundance of very labile compounds, such as proteins, sugars and PUFAs in S_1 sediment confirmed this recycling efficiency. Moreover, it is very probable that the natural mineral matrix of Lake Créteil sediment (such mineral matrix was negligible in S_2 enclosures) contained much more P-binding elements, such as iron oxides, which should have favoured a higher retention of phosphorus in the well-oxygenated conditions of the experiment (Mortimer, 1941).

Whatever the treatments, the highest biomass of seston was observed in February and in March, when the biomass and abundance of zooplankton were the lowest. This seasonal trend, previously observed (Danger *et al.*, 2012), agrees with the low grazing activity of zooplankton in late winter, which results in a weak top-down control on phytoplankton. On the other hand, the enhanced grazing activity of zooplankton in spring probably resulted in a more important top-down control on phytoplankton (Sarnelle, 1999).

The bottom-up effect observed for S_2 treatment did not strongly influence the structure of the zooplankton community. The only effect was observed within Cladocera. The typically pelagic daphniidae tended to be less abundant, while the benthic and littoral Chydoridae attained higher densities in the S_2 enclosures. The observed increase in the abundance of Chydoridae in the S_2 enclosures, characterized by their OM-rich sediment, is consistent with the ability of Chydoridae to ingest detritus (de Eyto & Irvine, 2001). Indeed, some Chydoridae, such as *Chydorus* sp., present in the enclosures, are able to use both benthic and open-water food sources (de Eyto & Irvine, 2001). Finally, after a strong increase in the beginning of spring, the biomass of zooplankton from S_2 treatment slowly decreased in the end of spring, suggesting that phytoplankton became rapidly limiting for zooplankton growth in spite of the initial positive bottom-up effect from this sediment. This result supports the

hypothesis that competition for food might be important for herbivorous zooplankton in such experimental systems when external nutrient loading is absent.

The occurrence of a bottom-up effect of S_2 treatment is also supported by the elemental composition of seston. The higher N content of seston observed in S_2 treatment, compared to S_0 and S_1 ones, suggests a release of N from this "labile" sediment. The lower C/N ratio of seston from S_2 enclosures, probably indicative of a higher nutritional value (Jones *et al.*, 2002), could have contributed to the higher biomass of zooplankton observed in these enclosures. By contrast, zooplankton C/N ratios did not depend on treatments and were quite similar to those obtained by Danger *et al.* (2012). Since species composition of zooplankton was only slightly affected by sediment treatments, this constant C/N ratio is in agreement with the homeostasis constraints on zooplankton stoichiometry. Indeed, zooplankton species have specific elemental compositions (Hessen, 1990; Andersen & Hessen, 1991). Moreover, the decrease in zooplankton C/N ratio with time observed in the enclosures is in agreement with the increase in copepods within the community. As a conclusion, changes in seston stoichiometric ratios do not necessarily induce changes in the structure of the zooplankton community. In a previous study, Danger *et al.* (2012) had shown that changes at the top of the food web affected elemental composition of zooplankton communities by shifting species dominance, but did not affect seston stoichiometric ratios. This suggests that stoichiometric changes are not necessarily transferred up or down along food chains within pelagic food webs.

Although addition of sediment influenced seston stoichiometry, we did not observe any significant influence of the sediment treatments on its lipid composition. On the other hand, previous studies (Allard *et al.*, 2011, Danger *et al.*, 2012) showed that changes in biochemical composition of seston could occur despite similar elemental ratios. This strengthens the conclusion of these authors that both elemental and biochemical compositions

of OM might provide useful information for understanding links between food-web structure and functioning of aquatic ecosystems.

Even if controversies do exist about the importance of internal nutrient loading and the various mechanisms that allow the release of resources from sediments to the overlaying water (see Nürnberg, 2009), our results show that:

(i) sediments with a high abundance of labile OM, which are more typical of eutrophic ecosystems, may clearly foster the pelagic food webs even after the reduction of allochthonous inputs and even in absence of anoxia (Søndergaard *et al*., 2007);

(ii) sediments with low OM contents and biodegradability, typical of oligo-mesotrophic ecosystems, are necessary for reducing (at least in absence of anoxia) delayed bottom-up forcing of sediment on the pelagic compartments.

Effects of bottom-up forcing on recent sediments

The higher biomass of both seston and zooplankton observed in S_2 enclosures did not induce significant higher sedimentation rates in these enclosures. This might be due to low production of sinking material from seston and zooplankton in pelagic systems characterized by the absence of fish. Indeed, the values obtained in this study are in agreement with those from previous studies carried out in zooplankton-dominated systems (Sarnelle, 1999; Danger *et al.*, 2012). These studies showed that the sedimentation rates are lower in systems dominated by zooplankton than in presence of fish. As a consequence, even if differences in sedimentation rates may have existed, they were probably low and hardly detectable in such fishless and shallow systems.

In our enclosures, the biomass of seston was higher than that of zooplankton. Moreover, phytoplankton, which constitutes up to 40% of seston (Hessen *et al.*, 2003), is known to sink much more than zooplankton (Sommer, 1984). Thus, changes in the elemental composition of seston observed in the different treatments are expected to result in similar changes in recent sediment. This hypothesis was not supported by the stoichiometric analyses since the elemental composition of recent sediment from S_2 treatment was similar to that from S_0 treatment. Surprisingly, the elemental composition of recent sediment from S_1 treatment differed from that of recent sediment from S_0 and S_2 treatments. At the present time, no explanation can be put forward for these results.

Apart from chlorophyll-derived compounds, no differences in the relative amounts of lipid classes of recent sediment were observed between the treatments. The higher relative abundances of chlorophyll-derived compounds in recent sediment from S_2 treatment probably indicate a higher contribution of phytoplankton to this sediment. The relative abundances of both FAs and sterols in the recent sediment ranged between those observed for seston and zooplankton. These results suggest that both seston and zooplankton noticeably contributed to recent sediment. The relative contribution of each pelagic compartment is difficult to estimate. As the relative abundances of long-chain PUFAs of recent sediments were quite low, and more similar to those observed for seston than to those observed for zooplankton, this suggest a rather low contribution of zooplankton to recent sediment. However, PUFAs are highly sensitive to bacterial degradation (Cranwell, 1981) and likely do not survive unaltered for a long time in the water column. Consequently, on the basis of PUFA concentrations, zooplankton contribution to recent sediment could be underestimated.

The low amounts of bacterial FAs suggest a rather low contribution of bacteria to recent sediments. Nevertheless, stanols were present in higher relative amounts in recent sediments than in seston and in zooplankton. This indicates that the degradation of settling

organic matter occurred even at the very short time scales (ca. 1 week) of this experiment. However, the relative amounts of unsaturated fatty acids, the most reactive compounds towards biodegradation, were rather high in recent sediments. This suggests that microbial reworking was limited for these very recent sediments.

Lipid biomarkers such as PUFAs and bulk parameters such as sugar and protein contents have been used to estimate and compare the quality of sediments (Canuel *et al.*, 2007; Allard *et al.*, 2011). In the present study, these indicators did not reveal any relationship between the quality of the added sediment and that of the recently deposited one. Finally, the comparison between this study and those dealing with top-down effects (Canuel *et al.*, 2007; Allard *et al.*, 2011; Danger *et al.*, 2012) suggests that the quantity and the quality of settling organic matter in aquatic ecosystems are less affected by bottom-up forces (linked to sediment quality) than by top-down forces (linked to food-web structure) and calls for a factorial approach on these two parameters.

Conclusion

This mesocosm experiment demonstrates that the origin and the quality of lake sediment can result in changes in the pelagic compartments. The release of nutrients and OM from the sediment to the water column can induce a bottom-up forcing transferred from seston to zooplankton by means of trophic interactions. However, this effect is substantial only when sediment OM is highly biodegradable and typical of eutrophic systems with high abundances of omnivorous and planktivorous fish (Banas *et al.*, 2008; Yokoyama *et al.*, 2009). This strengthens the suggestion of Harrault *et al.* (2012) that maintaining over a sufficiently long period a top-down control of phytoplankton biomass, for example through the

biomanipulation of fish communities, should not only induce a more efficient grazing on primary producers, but should also reduce the quantity and biodegradability of SOM, ultimately decreasing internal nutrient cycling. The progressive reduction of internal recycling might explain the acknowledged efficiency of biomanipulations for improving water quality (Jeppesen *et al.*, 2007).

Finally, microcosms and mesocosms have been frequently criticized for their lack of realism (Carpenter, 1996; Schindler, 1998). Our results suggest that the absence of initial sediment in most realized mesocosm experiments did not necessarily induce major biases in the functioning of pelagic systems, and tend to confirm the ecological significance of the effects identified by such manipulations (Spivak & Vanni, 2011). However, it should be kept in mind that other benthic processes, such as redox and pH conditions controlling phosphorus release, or sediment as a source of planktonic organisms and macroinvertebrates, might also strongly impact biogeochemical cycles (Søndergaard *et al.*, 2003). Their importance could be underestimated in most mesocosm experiments.

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Table 1: Selection criteria for the choice of the initial sediments. Elemental and biochemical composition (n = 1)

	C [a]	OC [a]	N [a]	OC/N	Sugars [a]	Proteins [a]	PUFAs [b]
S_1	5.7	0.9	0.1	9.0	0.1	0.1	4.9
S_2	23.1	9.7	2.4	4.0	0.7	1.5	12.6

[a] % of dry weight

[b] % of total fatty acids.

Table 2 Nutrient (µg/L) concentrations of water sampled in May and June 2010 and DOC (mg/L) concentrations of water sampled in May. Biomass (mg L^{-1}), elemental and biochemical compositions (% of dry weight) of seston, zooplankton (sampled from February to June 2010). Sedimentation rates (g DW m^{-2} d^{-1}), elemental and biochemical compositions (% of dry weight) of recent sediments (sampled in May and June 2010). Significant effects are in bold. Tukey's post-hoc tests were performed when the effect of sediment treatment was significant with the LME test.

	Means ± SD			Statistics							
	Treatment			Sediment						Time	Sediment × Time
				LME			Tukey (P values)				
	S_0	S_1	S_2	P values	DF [a]	F values	S_0-S_1	S_0-S_2	S_1-S_2	P values	P values
Water											
Ammonium	28.5 ± 22.7	22.9 ± 22.1	32.7 ± 22.7	0.39	2, 21	0.98	-	-	-	**0.001**	0.52
Nitrates	4.6 ± 3.8	4.1 ± 2.2	4.5 ± 3.5	0.90	2, 21	0.10	-	-	-	**< 0.001**	0.34
Phosphates	3.1 ± 5.3	3.8 ± 5.5	11.3 ± 10.3	**0.01**	2, 21	5.21	0.96	**0.01**	**0.02**	0.35	0.62
IN/P [b]	16 ± 21	18 ± 21	5 ± 5	0.24	2, 21	1.52	-	-	-	**< 0.01**	0.35
DOC	4.6 ± 0.9	4.3 ± 0.9	5.8 ± 1.2	**0.02**	2	5.01	0.80	0.07	**0.02**	-	-
Seston											
Biomass	1.18 ± 0.63	1.40 ± 1.03	2.14 ± 1.49	**< 0.005**	2, 21	6.92	0.57	**0.001**	**0.03**	**< 0.0001**	0.11
C	30.3 ± 8.6	29.3 ± 8.8	32.2 ± 8.6	0.27	2, 21	1.39	-	-	-	**< 0.001**	0.76
N	4.6 ± 1.9	4.7 ± 1.4	5.5 ± 1.5	**0.03**	2, 21	4.12	0.89	**0.02**	0.07	0.80	0.18
C/N ratio	6.6 ± 1.1	6.2 ± 1.0	5.9 ± 1.3	**< 0.005**	2, 21	8.06	**0.03**	**< 0.0001**	0.12	**< 0.0001**	**< 0.0001**
Zooplankton											
Biomass	0.27 ± 0.16	0.29 ± 0.19	0.51 ± 0.34	**0.002**	2, 21	8.87	0.99	**< 0.0001**	**< 0.0001**	**< 0.0001**	**0.002**

C	42.8 ± 8.8	42.7 ± 4.6	44.3 ± 4.2	0.52	2, 21	0.67	-	-	-	**< 0.01**	0.84
N	7.9 ± 2.6	8.9 ± 2.0	8.0 ± 1.7	0.66	2, 21	0.43	-	-	-	**< 0.0001**	0.23
C/N ratio	5.4 ± 2.1	5.3 ± 1.4	5.3 ± 1.2	0.94	2, 21	0.06	-	-	-	**< 0.0001**	0.06
Recent sediment											
Sedimentation rate	0.77 ± 0.40	1.42 ± 0.96	1.17 ± 0.53	0.13	2, 21	2.25	-	-	-	0.09	0.65
C	24.8 ± 2.7	15.5 ± 3.7	26.9 ± 2.6	**0.0001**	2, 21	14.22	**< 0.001**	0.43	**< 0.0001**	**0.03**	0.10
N	2.8 ± 0.7	1.5 ± 0.5	3.3 ± 0.4	**< 0.0001**	2, 21	22.61	**< 0.005**	0.12	**< 0.0001**	0.97	0.65
C/N ratio	9.1 ± 2.4	10.3 ± 1.8	8.0 ± 1.1	**< 0.005**	2, 21	8.41	**0.04**	0.37	**< 0.001**	0.17	0.95
OC [c]	23.9 ± 2.6	14.4 ± 5.8	27.3 ± 2.2	**0.02**	2	8.93	**0.05**	0.58	**0.01**	-	-
OC/N [c]	8.9 ± 1.1	9.6 ± 5.8	8.0 ± 0.8	0.94	2	0.06	-	-	-	-	-
Sugars [c]	3.3 ± 0.3	2.7 ± 1.2	3.2 ± 0.8	0.36	2	1.22	-	-	-	-	-
Proteins [c]	2.2 ± 0.3	1.8 ± 0.6	3.2 ± 0.9	0.78	2	0.25	-	-	-	-	-

[a] Degrees of Freedom

[b] Inorganic Nitrogen (sum of ammonium and nitrates)/Phosphates ratio

[c] analyses were performed only on sediments sampled in May 2010

Table 3 Mean lipid composition of seston, zooplankton and recent sediment sampled in May 2010. Statistical analyses were performed on the mean of the three sediment treatments for each compartment (mean ± SD; n = 9 for seston, zooplankton and recent sediment). Bold values indicate significant differences between seston, zooplankton and/or recent sediment. Total was expressed as % of total lipids. Sub-classes of fatty acids and sterols were expressed as % of total fatty acids and sterols, respectively.

	FAs					Sterols				OHs	OH-FAs	CHLOs
Mean	Total	SAFA	MUFA	PUFA	BACTFA	Total	$C_{27}\Delta^5$	$C_{29}\Delta^5$	Stanols	Total	Total	Total
Seston	**75.4 ± 9.3**	**74.2 ± 5.4**	**11.9 ± 4.4**	**4.2 ± 2.8**	**9.7 ± 1.5**	5.2 ± 2.0	**23.5 ± 10.8**	**57.2 ± 16.0**	**0.9 ± 0.6**	**14.5 ± 6.9**	**4.2 ± 1.2**	**0.5 ± 0.1**
Zooplankton	**87.3 ± 7.0**	**52.8 ± 5.3**	**21.5 ± 5.3**	**19.4 ± 4.9**	**6.4 ± 1.2**	6.0 ± 4.6	**68.1 ± 11.0**	**21.5 ± 11.0**	**1.2 ± 0.8**	**3.9 ± 2.9**	**1.3 ± 0.6**	**1.3 ± 0.8**
Recent sediment	**75.0 ± 7.7**	**56.2 ± 3.2**	**24.0 ± 2.2**	**11.1 ± 2.5**	**8.7± 1.9**	6.8 ± 4.1	**34.1 ± 7.1**	**43.9 ± 9.5**	**2.3 ± 0.9**	**10.5 ± 3.7**	**4.6 ± 1.1**	**2.8 ± 1.7**

FAs: fatty acids, SAFA: saturated fatty acid, MUFA: monounsaturated fatty acid, PUFA: polyunsaturated fatty acid, BACTFA: bacterial fatty acid = Σ 15 :0 + Σ 17 :0 + branched-chain FAs, OHs: *n*-alkanols, OH-FAs: sum of α-, β- and ω-hydroxy acids, CHLOs: chlorophyll-derived compounds.

Table 4 Mean specific composition of zooplankton communities (Individual L^{-1}) sampled in February and May 2010. Mean ± SD. For each treatment and each date, counting was only performed on triplicates. Significant effects are in bold.

	Means ± SD			Statistics							
	Treatment			Sediment						Time	Sediment × Time
				LME			Tukey (P values)				
	S_0	S_1	S_2	P values	DF [a]	F values	S_0-S_1	S_0-S_2	S_1-S_2	P values	P values
Rotifers	2.8 ± 2.8	1.7 ± 1.2	7.2 ± 15.4	0.86	2, 6	0.15	-	-	-	0.23	**0.002**
Cladocerans											
Daphnia	23.4 ± 22.2	11.4 ± 13.7	3.4 ± 4.2	0.11	2, 6	3.27	-	-	-	**0.066**	**0.24**
Ceriodaphnia	1.1 ± 2.2	0.1 ± 0.3	0.0 ± 0.1	0.18	2, 6	2.33	-	-	-	**0.0008**	**0.0054**
Bosminidae	1.3 ± 1.7	2.2 ± 3.9	2.2 ± 4.4	0.95	2, 6	0.05	-	-	-	**< 0.0001**	0.94
Chydoridae	5.6 ± 6.2	2.8 ± 3.7	16.5 ± 23.3	**0.016**	2, 6	8.87	0.76	**0.02**	**< 0.005**	**< 0.0001**	**< 0.0001**
Copepods											
Cyclopids	13.0 ± 14.0	7.5 ± 11.0	12.1 ± 12.5	0.33	2, 6	1.34	-	-	-	**< 0.0001**	0.67
Calanoids	16.6 ± 10.8	10.3 ± 16.5	15.7 ± 18.6	0.41	2, 6	1.04	-	-	-	**0.0001**	**0.0008**
Nauplii	111.9 ± 111.5	61.0 ± 65.1	99.2 ± 124..0	0.11	2, 6	2.22	-	-	-	0.066	0.24

[a] Degrees of Freedom

Figure captions:

Figure 1: Seasonal variations of seston (a) and zooplankton (b) biomass and sedimentation rates (c) (mean ± SE). White, grey and black bars represent the control treatment (S_0), S_1 and S_2 treatments respectively. Significant effects of time are represented by different letters.

Figure 2: Seasonal variations of carbon (a) and nitrogen (b) contents and C:N ratio (c) of the seston (mean ± SE). White, grey and black bars represent the control treatment (S_0), S_1 and S_2 treatments respectively. Significant effects of time are represented by different letters.

Figure 3: Seasonal variations of carbon (a) and nitrogen (b) contents and C:N ratio (c) of the zooplankton (mean ± SE). White, grey and black bars represent the control treatment (S_0), S_1 and S_2 treatment respectively. Significant effects of time are represented by different letters.

Figure 4: Variations of carbon (a) and nitrogen (b) contents and C:N ratio (c) of the short-term sediment (mean ± SE). White, grey and black bars represent the control treatment (S_0), S_1 and S_2 treatment respectively. Significant effects of time are represented by different letters.

Figure 1

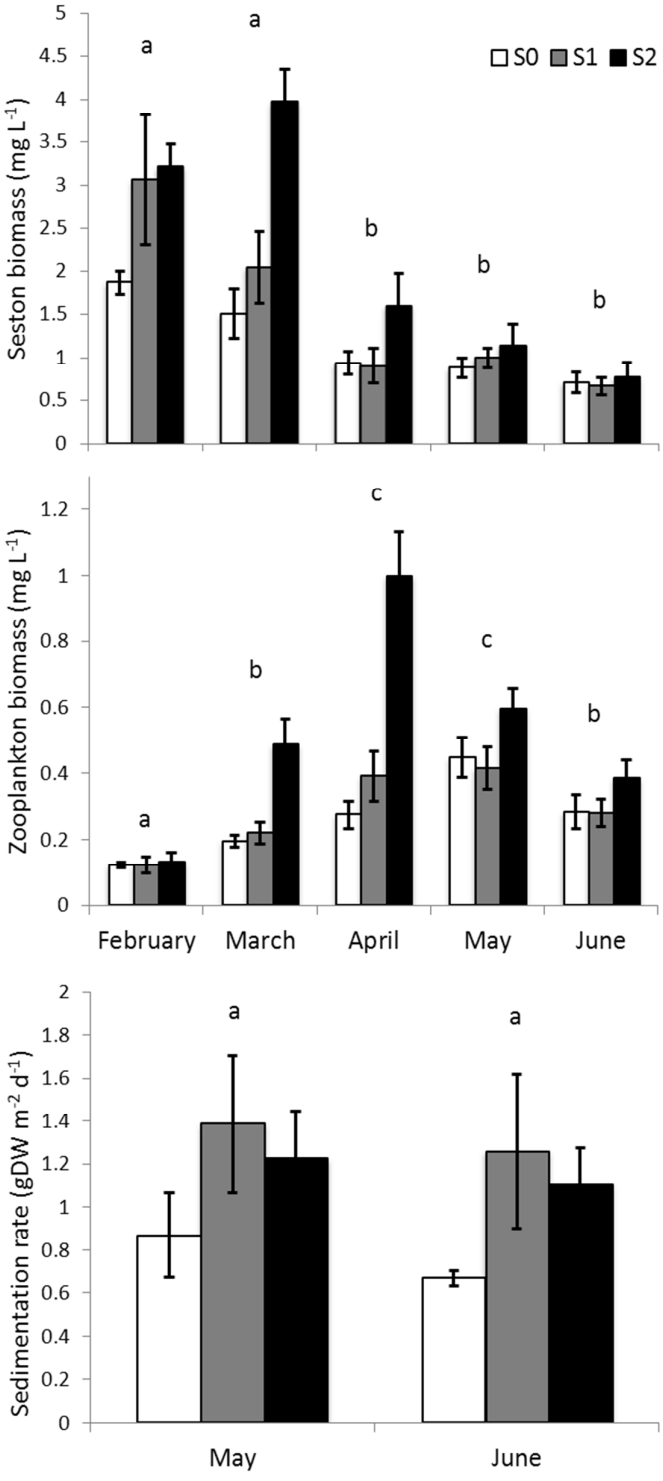

S0 S1 S2
Seston biomass (mg L-1)
Zooplankton biomass (mg L-1)
Sedimentation rate (gDW m-2 d-1)
a
a
b
b
b
a
b
c
c
b
a
a
February
March
April
May
June
May
June

Figure 2

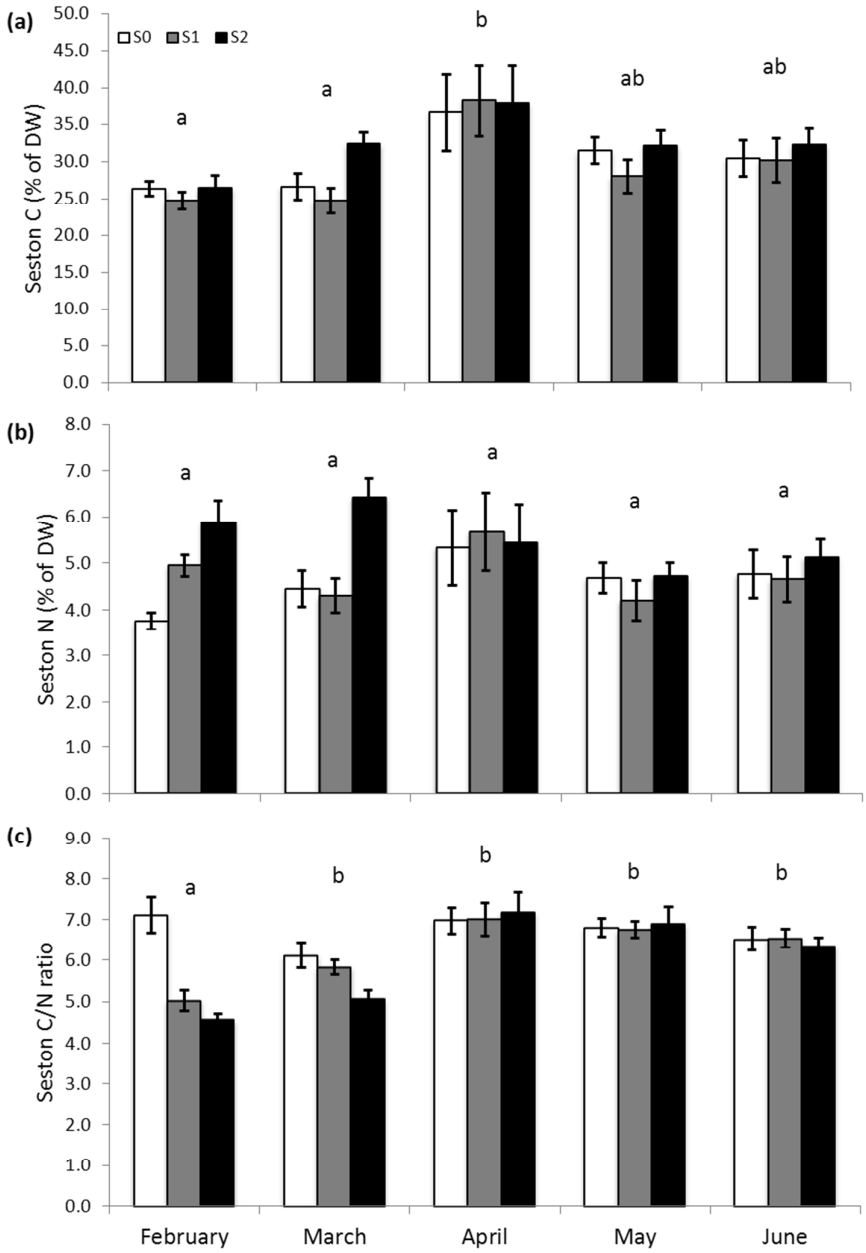

(a)
S0 S1 S2
Seston C (% of DW)
50.0
45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
a
a
b
ab
ab
(b)
Seston N (% of DW)
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
a
a
a
a
a
(c)
Seston C/N ratio
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
a
b
b
b
b
February
March
April
May
June

Figure 3

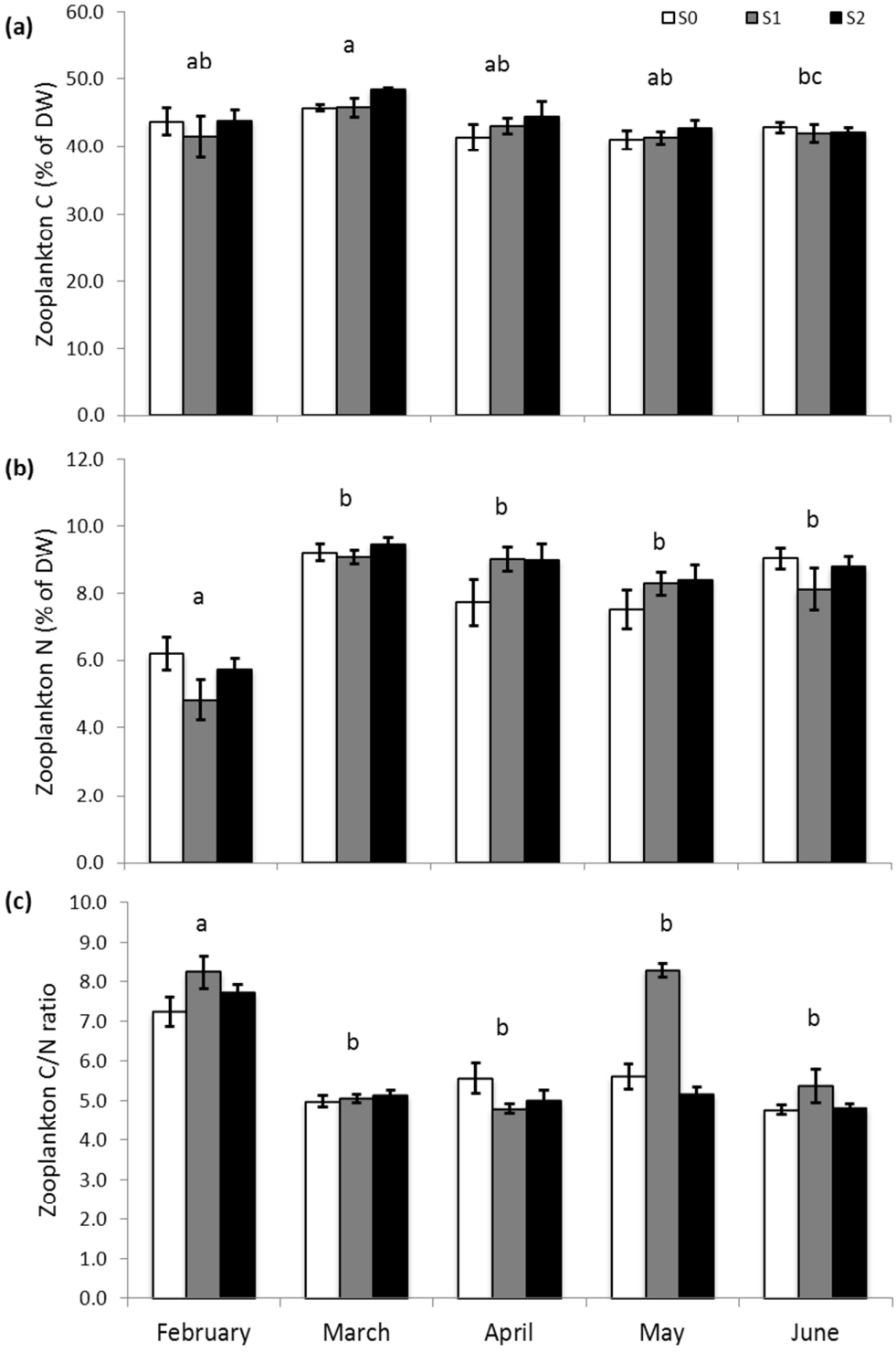
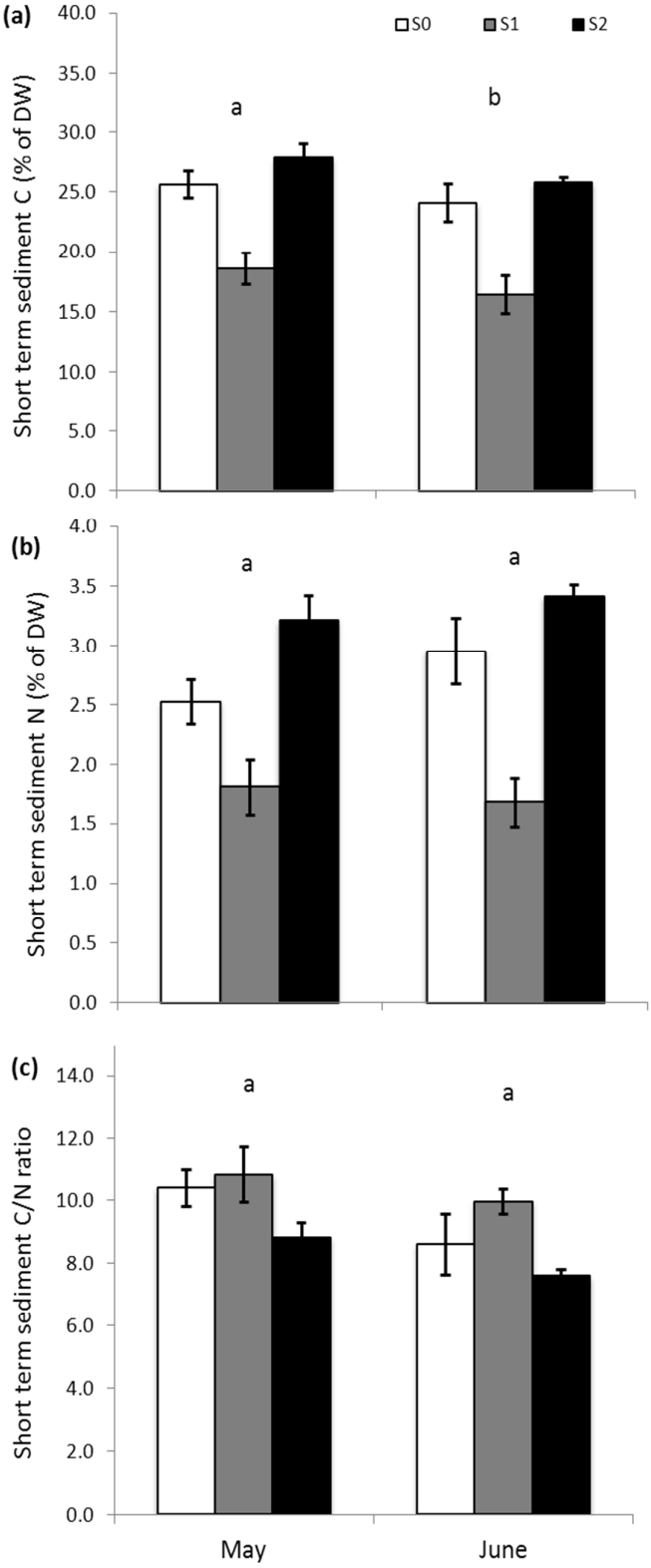

(a)
S0
S1
S2
Zooplankton C (% of DW)
60.0
50.0
40.0
30.0
20.0
10.0
0.0
ab
a
ab
ab
bc
(b)
Zooplankton N (% of DW)
12.0
10.0
8.0
6.0
4.0
2.0
0.0
a
b
b
b
b
(c)
Zooplankton C/N ratio
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
a
b
b
b
b
February
March
April
May
June

Figure 4


(a)
S0
S1
S2
Short term sediment C (% of DW)
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
a
b
(b)
Short term sediment N (% of DW)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
a
a
(c)
Short term sediment C/N ratio
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
a
a
May
June

Supplementary Table 1 Lipid composition of the initial sediments. Total was expressed as % of total lipids. Sub-classes of fatty acids, sterols, alkanols and hydroxy acids were expressed as % of total fatty acids, sterols, alkanols and hydroxy acids, respectively.

	FAs					Sterols				OHs			OH-FAs			CHLOs
	Total	SAFA	MUFA	PUFA	BACTFA	Total	$\Sigma\Delta^5$	$\Sigma\Delta^7$	stanols	Total	SC	LC	Total	α + β	ω	Total
S_1	36.4	74.2	13.9	4.9	6.6	16.0	61.2	ND	38.8	26.3	5.1	94.9	8.5	71.4	26.9	4.5
S_2	48.2	64.9	17.6	12.6	3.9	19.0	30.1	24.6	28.2	13.4	1.7	98.3	2.4	100.0	ND	9.8

FAs: fatty acids, SAFA: saturated fatty acid, MUFA: monounsaturated fatty acid, PUFA: polyunsaturated fatty acid, BACTFA: bacterial fatty acid = Σ 15 :0 + Σ 17 :0 + branched-chain FAs, $\Sigma\Delta^5$: sum of Δ^5-sterols, $\Sigma\Delta^7$: sum of Δ^7-sterols, OHs: alkanols, SC: short-chain alkanols (carbon number ≤ 18), LC: long-chain alkanols (carbon number ≥ 20), OH-FAs: hydroxy acids, α + β: sum of α- and β-hydroxy acids, ω: ω-hydroxy acids, CHLOs: chlorophyll-derived compounds, ND: non detected.

The quality (potential biodegradability) of the initial sediments was estimated using their contents in the constituents which were preferentially degraded by bacteria ie., proteins, sugars and PUFAs. The degradation state of these sediments was estimated using their contents in compounds related to the presence of bacteria ie. BACTFAs (Wakeham & Beier, 1991; Budge & Parrish, 1998) or to the bacterial activity ie. α- and β-OH-FAs (Cranwell, 1981), and stanols, the saturated homologues of sterols (Gaskell & Eglinton, 1975).

The high relative abundance of Δ^7-sterols in S_2 is consistent with the high contribution of Chlorophyceae to S_2 observed previously (Danger *et al.*, 2012). Indeed, these sterols are abundant in many Chlorophyceae (Volkman, 1986), and have been proposed as indicators of these algae (Cranwell, 1982). In contrast, Δ^7-sterols were not detected in S_1. 24-methyl- and 24-ethyl-cholest-5-enols, present in high amounts in S_1, are abundant in algae and in vascular plants as well. So, the sterol distribution of S_1 cannot allow to discriminate between autochthonous and allochthonous inputs. The higher relative abundances of chlorophyll-derived compounds in S_2 than in S_1 corroborate also a higher phytoplanktonic contribution to S_2. Indeed, such chlorophyll-derived compounds are usually considered as arising from the biodegradation of the phytyl side-chain of chlorophyll (Rontani &Volkman, 2003).

The higher relative amounts of BACTFAs in S_1 than in S_2 suggest that S_1 was in a more advanced degradation state than S_2. This is supported by higher amounts of α- and β-OH-FAs and stanols in S_1 than in S_2. Indeed, α- and β-OH-FAs are usually related to microbial input in sediment (Cranwell, 1981), and stanols, the saturated homologues of sterols, are usually considered as formed through in situ microbial reduction of sterols (Gaskell & Eglinton, 1975).

Supplementary Table 2 Fatty acid composition (% of total fatty acids) of the initial sediments S_1 and S_2 (n = 1).

SAFA	S_1	S_2	**MUFA**	S_1	S_2	**PUFA**	S_1	S_2	**BACT**	S_1	S_2
14:0	1.3	0.8	16:1ωx	tr	tr	16:3ω3	ND	0.4	14:0 br	0.0	0.2
16:0	12.4	10.7	16:1ω7	5.1	1.7	16:2ωx	ND	0.9	15:0[a]	2.9	2.0
18:0	8.4	3.2	18:1ω9	4.8	9.5	18:3ω6	0.0	0.3	16:0 br	0.4	0.4
20:0	3.2	1.0	18:1ω7	3.0	2.8	18:4ω3	0.0	0.3	17:0[a]	3.2	1.3
21:0	0.7	0.2	18:1ωx	0.0	0.7	18:2ω6 (LIN)	1.0	1.6			
22:0	5.4	6.1	20:1ω9	0.9	1.2	18:3ω3 (ALA)	1.6	7.8			
23:0	1.8	0.5	22:1ωx	0.0	0.2	20:4ω6 (ARA)	0.9	0.3			
24:0	12.6	9.7	24 :1ωx	0.0	0.5	20:5ω3 (EPA)	1.4	0.9			
25:0	1.6	0.7	26 :1ωx	0.0	0.8	22:5ω6	tr	0.1			
26:0	10.7	17.1				22:6ω3 (DHA)	tr	0.1			
27:0	1.2	0.9									
29:0	0.5	0.0									
30:0	2.9	1.5									
Subtotal	74.2	64.9		13.9	17.6		4.9	12.6		6.6	3.9
Σshort-chain	22.1	14.7				Σshort-chain	2.6	11.2			
Σlong-chain	52.1	50.2				Σlong-chain	2.3	1.4			

x: unknown position of double bounds. br: branched-chain FA. tr: traces, LIN: linoleic acid, ALA: α-linolenic acid, ARA: arachidonic acid, EPA: eicosapentaenoic acid, DHA: docosahexaenoic acid. [a] Sum of branched and linear FAs.

Supplementary Table 3 Fatty acid composition (% of total FAs) of seston, zooplankton and recent sediment sampled in May 2010 (mean ± SD; n = 3).

FA	Seston			Zooplankton			Recent sediment		
	S_0	S_1	S_2	S_0	S_1	S_2	S_0	S_1	S_2
SAFA									
12:0	0.4 ± 0.2	0.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.3 ± 0.1	0.2 ± 0.1	0.4 ± 0.2
14:0	4.1 ± 1.8	5.3 ± 2.5	3.2 ± 0.4	6.0 ± 5.1	7.2 ± 5.3	3.6 ± 1.4	2.4 ± 0.6	3.1 ± 1.5	3.0 ± 1.7
16:0	41.6 ± 3.3	40.6 ± 3.6	40.7 ± 2.7	32.1 ± 1.3	34.6 ± 2.0	36.7 ± 2.5	35.6 ± 1.7	33.5 ± 4.0	34.0 ± 2.3
18:0	17.5 ± 0.4	17.1 ± 4.0	19.3 ± 2.5	8.7 ± 0.7	11.3 ± 1.3	9.3 ± 0.8	11.6 ± 1.2	12.0 ± 0.9	9.6 ± 1.6
20:0	1.6 ± 0.1	1.6 ± 0.4	1.9 ± 0.2	0.5 ± 0.1	0.8 ± 0.2	0.5 ± 0.1	0.9 ± 0.8	1.6 ± 0.1	1.0 ± 0.2
21:0	0.5 ± 0.1	0.6 ± 0.2	0.6 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.2 ± 0.2	0.3 ± 0.0	0.2 ± 0.1
22:0	3.1 ± 0.0	3.6 ± 1.8	4.0 ± 0.2	0.8 ± 0.3	1.4 ± 0.5	0.7 ± 0.1	1.5 ± 1.5	3.2 ± 1.1	1.6 ± 1.1
23:0	0.7 ± 0.0	0.9 ± 0.5	0.9 ± 0.1	0.2 ± 0.0	0.3 ± 0.1	0.1 ± 0.0	0.3 ± 0.3	0.4 ± 0.2	0.3 ± 0.2
24:0	1.2 ± 0.2	1.5 ± 1.0	1.6 ± 0.3	0.3 ± 0.1	0.5 ± 0.4	0.2 ± 0.1	0.9 ± 0.9	1.2 ± 0.6	0.8 ± 0.4
25:0	0.3 ± 0.1	0.5 ± 0.4	0.5 ± 0.2	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.2 ± 0.2	0.2 ± 0.1	0.1 ± 0.1
26:0	0.3 ± 0.2	0.4 ± 0.4	0.4 ± 0.2	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	0.5 ± 0.7	0.6 ± 0.5	0.5 ± 0.4
27:0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
28:0	0.5 ± 0.4	0.7 ± 0.8	0.9 ± 0.7	0.1 ± 0.1	0.3 ± 0.3	0.1 ± 0.1	1.2 ± 1.1	0.2 ± 0.1	0.4 ± 0.4
30:0	0.5 ± 0.6	0.7 ± 0.9	0.7 ± 0.8	0.1 ± 0.1	0.3 ± 0.4	0.1 ± 0.1	1.3 ± 1.4	0.5 ± 0.8	1.8 ± 3.0
32:0	0.2 ± 0.1	0.2 ± 0.2	0.3 ± 0.3	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.2	0.1 ± 0.1

Subtotal	72.6 ± 3.8	74.3 ± 9.5	75.6 ± 2.5	49.3 ± 2.8	57.3 ± 7.0	51.8 ± 2.4	57.2 ± 2.0	57.5 ± 2.2	54.1 ± 4.5
Σshort-chain	63.6 ± 5.0	63.4 ± 3.8	63.7 ± 5.0	47.1 ± 3.3	53.2 ± 8.5	49.8 ± 3.1	49.9 ± 2.8	48.8 ± 6.4	47.1 ± 3.9
Σlong-chain	9.0 ± 1.6	10.9 ± 6.6	12.0 ± 2.7	2.2 ± 0.8	4.1 ± 2.2	2.0 ± 0.7	7.3 ± 4.4	8.8 ± 4.2	7.0 ± 5.8
MUFA									
15:1ωx	0.5 ± 0.2	0.4 ± 0.2	0.3 ± 0.2	0.2 ± 0.1	0.4 ± 0.3	0.5 ± 0.1.	0.2 ± 0.1	0.4 ± 0.1	0.6 ± 0.5
16:1ω7	3.6 ± 1.3	4.1 ± 2.9	3.3 ± 0.8	4.1 ± 0.6	3.9 ± 1.5	5.2 ± 2.4	4.4 ± 0.3	4.8 ± 1.9	5.1 ± 1.7
16:1ωx	0.2 ± 0.3	0.1 ± 0.1	0.3 ± 0.2	0.4 ± 0.1	1.0 ± 0.5	1.2 ± 0.4	1.5 ± 0.3	1.5 ± 0.6	2.5 ± 0.5
17:1ωx	0.3 ± 0.5	0.1 ± 0.1	0.0 ± 0.0	0.4 ± 0.1	0.3 ± 0.2	0.4 ± 0.3	0.6 ± 0.2	0.6 ± 0.2	1.2 ± 0.6
18:1ω9	6.4 ± 1.6	2.3 ± 1.6	5.2 ± 0.7	10.0 ± 2.8	9.8 ± 2.1	9.4 ± 2.0	8.1 ± 0.9	10.6 ± 0.9	8.5 ± 0.7
18:1ω7	2.2 ± 2.0	0.9 ± 0.7	1.5 ± 1.3	5.2 ± 1.5	4.0 ± 2.4	6.2 ± 2.5	6.5 ± 0.8	4.3 ± 1.3	4.2 ± 0.6
18:1ωx	0.3 ± 0.4	1.7 ± 2.8	0.6 ± 1.1	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	2.9 ± 1.8
20:1ωx	0.2 ± 0.1	0.3 ± 0.2	0.2 ± 0.0	0.4 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.5 ± 0.3	0.4 ± 0.1
20:1ω9	0.1 ± 0.1	0.0 ± 0.1	0.2 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.1± 0.0
22:1ωx	0.1 ± 0.2	0.2 ± 0.4	0.0 ± 0.1	0.0 ± 0.1	0.0 ± 0.1	0.0 ± 0.1	0.7 ± 0.9	0.3 ± 0.3	0.1 ± 0.1
Subtotal	13.9 ± 3.2	10.2 ± 7.3	11.8 ± 1.8	21.1 ± 4.4	19.9 ± 5.7	23.5 ± 7.0	22.9 ± 1.5	23.5 ± 0.4	25.6 ± 3.2
PUFA									
16:xω3	0.1 ± 0.1	0.2 ± 0.2	ND	0.2 ± 0.1	0.1 ± 0.0	0.2 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.0
16:3ω3	0.1 ± 0.1	0.1 ± 0.1	ND	0.3 ± 0.1	0.2 ± 0.1	0.5 ± 0.0	0.3 ± 0.0	0.4 ± 0.2	0.7 ± 0.2
16:2ωx	0.0 ± 0.1	0.1 ± 0.1	ND	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.1	ND	ND	ND
18:3ω6	ND	ND	ND	0.3 ± 0.1	0.1 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.0

18:2ω3	0.5 ± 0.2	0.3 ± 0.2	0.1 ± 0.2	1.9 ± 0.6	1.0 ± 0.4	1.5 ± 1.1	0.8 ± 0.2	0.5 ± 0.2	0.4 ± 0.1
18:2ω6 (LIN)	1.5 ± 1.0	0.9 ± 0.6	0.8 ± 0.2	6.1 ± 1.7	5.4 ± 1.0	2.9 ± 0.7	5.7 ± 0.9	4.6 ± 1.5	3.4 ± 0.2
18:3ω3 (ALA)	1.7 ± 1.2	2.9 ± 3.5	1.4 ± 0.8	7.6 ± 2.5	4.6 ± 1.2	6.7 ± 1.7	3.5 ± 0.4	3.7 ± 1.8	4.1 ± 1.5
18:2ωx	0.3 ± 0.1	0.8 ± 0.5	0.7 ± 0.4	1.1 ± 1.0	0.4 ± 0.3	0.7 ± 0.2	0.4 ± 0.1	0.4 ± 0.2	0.4 ± 0.1
20:4ω6 (ARA)	0.1 ± 0.1	ND	0.0 ± 0.1	1.4 ± 0.3	1.1 ± 0.1	0.6 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
20:5ω3 (EPA)	0.0 ± 0.1	ND	0.0 ± 0.0	2.4 ± 0.7	1.6 ± 0.6	2.1 ± 1.1	0.2 ± 0.1	0.4 ± 0.1	0.3 ± 0.1
20:2ωx	ND	ND	ND	0.6 ± 0.1	0.4 ± 0.1	0.2 ± 0.1	ND	ND	0.1 ± 0.1
20:3ω3	ND	ND	ND	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
20:3ωx	ND	ND	ND	0.2 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1
22:5ω6	ND	ND	ND	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
22:6ω3 (DHA)	ND	ND	ND	1.3 ± 0.4	0.8 ± 0.5	1.0 ± 0.7	0.1 ± 0.1	0.0 ± 0.1	0.1 ± 0.0
22:5ω3	ND	ND	ND	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.0	ND	ND	ND
Subtotal	4.2 ± 2.2	5.3 ± 4.7	3.1 ± 1.1	24.1 ± 3.1	16.6 ± 2.0	17.3 ± 5.5	12.0 ± 1.4	10.9 ± 4.1	10.2 ± 1.6
Σshort-chain	4.1 ± 2.0	5.3 ± 4.7	3.0 ± 1.0	17.6 ± 2.3	12.1 ± 0.9	12.7 ± 3.3	11.3 ± 1.5	10.0 ± 3.8	9.3 ± 1.9
Σlong-chain	0.1 ± 0.2	0.0 ± 0.0	0.1 ± 0.1	6.5 ± 0.9	4.6 ± 1.3	4.5 ± 2.2	0.8 ± 0.1	0.9 ± 0.3	0.9 ± 0.3
BACTFA									
14:0 br	0.2 ± 0.1	0.1 ± 0.0	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.2
15:0 br	1.9 ± 0.6	2.3 ± 1.4	1.8 ± 0.2	1.8 ± 0.2	1.5 ± 0.2	2.2 ± 0.3	2.0 ± 0.3	2.3 ± 1.3	4.0 ± 1.8
15:0	2.0 ± 0.6	2.0 ± 0.1	1.9 ± 0.2	0.9 ± 0.1	1.3 ± 0.7	1.2 ± 0.2	1.4 ± 0.3	1.5 ± 0.4	1.9 ± 0.6
16:0 br	0.2 ± 0.0	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.1	0.2 ± 0.2	0.3 ± 0.1	0.5 ± 0.0	0.3 ± 0.1	0.5 ± 0.1

17:0 br	1.0 ± 0.2	1.1 ± 0.4	1.0 ± 0.4	0.7 ± 0.1	0.8 ± 0.3	1.2 ± 0.7	1.5 ± 0.9	1.2 ± 0.0	1.2 ± 0.2
17:0	3.4 ± 0.1	4.2 ± 0.4	3.8 ± 0.1	1.6 ± 0.1	2.0 ± 0.7	2.1 ± 0.7	2.1 ± 1.0	2.1 ± 0.2	1.8 ± 0.0
19:0	0.4 ± 0.2	0.3 ± 0.0	0.4 ± 0.1	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.3 ± 0.2	0.3 ± 0.1
Subtotal	9.3 ± 1.2	10.3 ± 2.7	9.5 ± 0.1	5.5± 0.1	6.1 ± 1.5	7.5 ± 1.0	7.9 ± 1.1	8.1 ± 1.7	10.1 ± 2.4

ND non detected. x: unknown position of double bounds. br: branched-chain FA

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